

25.1 Interactions among competing species shape ecological niches.

The Realized Niche

Each organism in an ecosystem confronts the challenge of survival in a different way. The **niche** an organism occupies is the sum total of all the ways it utilizes the resources of its environment. A niche may be described in terms of space utilization, food consumption, temperature range, appropriate conditions for mating, requirements for moisture, and other factors. *Niche* is not synonymous with **habitat**, the place where an organism lives. *Habitat* is a place, *niche* a pattern of living.

Sometimes species are not able to occupy their entire niche because of the presence or absence of other species. Species can interact with each other in a number of ways, and these interactions can either have positive or negative effects. One type of interaction is **interspecific competition**, which occurs when two species attempt to utilize the same resource when there is not enough of the resource to satisfy both. Fighting over resources is referred to as **interference competition**; consuming shared resources is called **exploitative competition**.

The entire niche that a species is capable of using, based on its physiological requirements and resource needs, is called the **fundamental niche**. The actual niche the species occupies is called its **realized niche**. Because of interspecific interactions, the realized niche of a species may be considerably smaller than its fundamental niche.

In a classic study, J. H. Connell of the University of California, Santa Barbara investigated competitive interactions between two species of barnacles that grow together on rocks along the coast of Scotland. Of the two species Connell studied, *Chthamalus stellatus* lives in shallower water, where tidal action often exposed it to air, and *Semibalanus balanoides* (called *Balanus balanoides* prior to 1995) lives lower down, where it is rarely exposed to the atmosphere (figure 25.2). In the deeper zone, *Semibalanus* could always outcompete *Chthamalus* by crowding it off the rocks, undercutting it, and replacing it even where it had begun to grow, an example of interference competition. When Connell removed *Semibalanus* from the area, however, *Chthamalus* was easily able to occupy the deeper zone, indicating that no physiological or other general obstacles prevented it from becoming established there. In contrast, *Semibalanus* could not survive in the shallow-water habitats where *Chthamalus* normally occurs; it evidently does not have the special adaptations that allow *Chthamalus* to occupy this zone. Thus, the fundamental niche of the barnacle *Chthamalus* included both shallow and deeper zones, but its realized niche was much narrower because *Chthamalus* was outcompeted by *Semibalanus* in parts of its fundamental niche. By contrast, the realized and fundamental niches of *Semibalanus* appear to be identical.

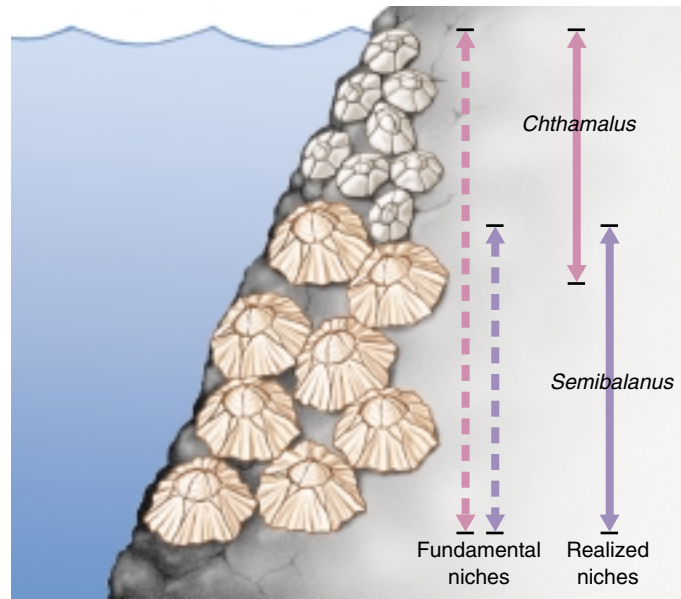


FIGURE 25.2

Competition among two species of barnacles limits niche use.

Chthamalus can live in both deep and shallow zones (its fundamental niche), but *Semibalanus* forces *Chthamalus* out of the part of its fundamental niche that overlaps the realized niche of *Semibalanus*.

Processes other than competition can also restrict the realized niche of a species. For example, a plant, the St. John's-wort, was introduced and became widespread in open rangeland habitats in California until a specialized beetle was introduced to control it. Populations of the plant quickly decreased and it is now only found in shady sites where the beetle cannot thrive. In this case, the presence of a predator limits the realized niche of a plant.

In some cases, the absence of another species leads to a smaller realized niche. For example, many North American plants depend on the American honeybee for pollination. The honeybee's population is currently declining for a variety of reasons. Conservationists are concerned that if the honeybee disappears from some habitats, the niche of these plant species will decrease or even disappear entirely. In this case, then, the absence—rather than the presence—of another species will be cause of a relatively small realized niche.

A niche may be defined as the way in which an organism utilizes its environment. Interspecific interactions may cause a species' realized niche to be smaller than its fundamental niche. If resources are limiting, two species normally cannot occupy the same niche indefinitely.

Gause and the Principle of Competitive Exclusion

In classic experiments carried out in 1934 and 1935, Russian ecologist G. F. Gause studied competition among three species of *Paramecium*, a tiny protist. All three species grew well alone in culture tubes, preying on bacteria and yeasts that fed on oatmeal suspended in the culture fluid (figure 25.3a). However, when Gause grew *P. aurelia* together with *P. caudatum* in the same culture tube, the numbers of *P. caudatum* always declined to extinction, leaving *P. aurelia* the only survivor (figure 25.3b). Why? Gause found *P. aurelia* was able to grow six times faster than its competitor *P. caudatum* because it was able to better utilize the limited available resources, an example of exploitative competition.

From experiments such as this, Gause formulated what is now called the **principle of competitive exclusion**. This principle states that if two species are competing for a limited resource, the species that uses the resource more efficiently will eventually eliminate the other locally—no two species with the same niche can coexist when resources are limiting.

Niche Overlap

In a revealing experiment, Gause challenged *Paramecium caudatum*—the defeated species in his earlier experiments—with a third species, *P. bursaria*. Because he expected these two species to also compete for the limited bacterial food supply, Gause thought one would win out, as had happened in his previous experiments. But that's not what happened. Instead, both species survived in the culture tubes; the

paramecia found a way to divide the food resources. How did they do it? In the upper part of the culture tubes, where the oxygen concentration and bacterial density were high, *P. caudatum* dominated because it was better able to feed on bacteria. However, in the lower part of the tubes, the lower oxygen concentration favored the growth of a different potential food, yeast, and *P. bursaria* was better able to eat this food. The fundamental niche of each species was the whole culture tube, but the realized niche of each species was only a portion of the tube. Because the niches of the two species did not overlap too much, both species were able to survive. However, competition did have a negative effect on the participants (figure 25.3c). When grown without a competitor, both species reached densities three times greater than when they were grown with a competitor.

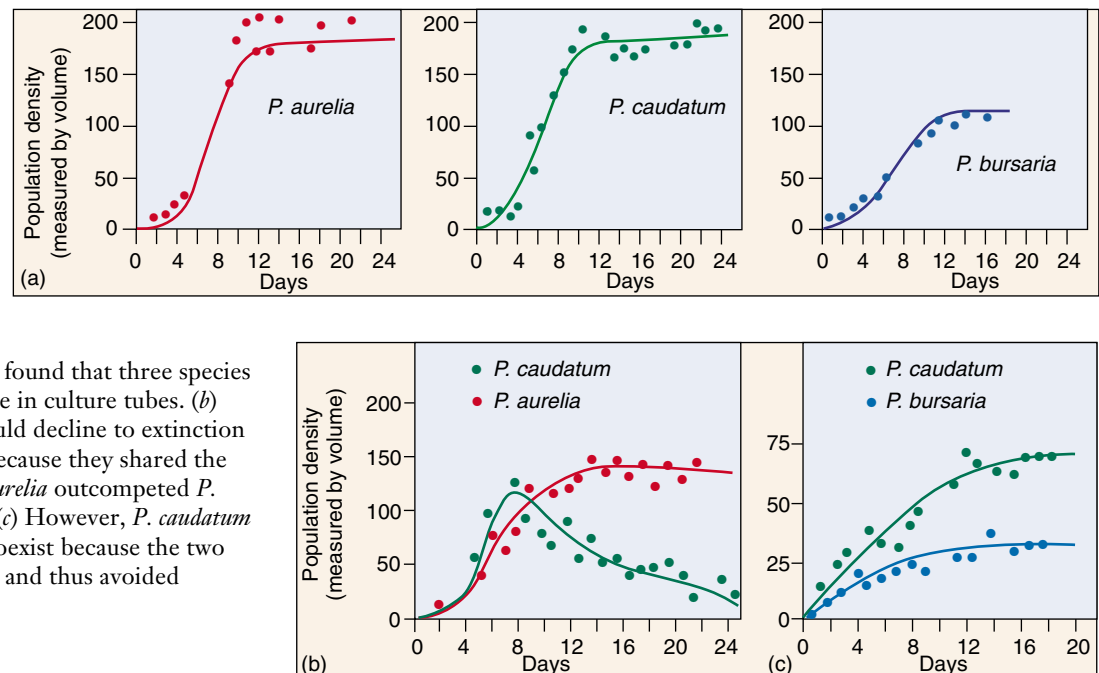
Competitive Exclusion

Gause's principle of competitive exclusion can be restated to say that *no two species can occupy the same niche indefinitely when resources are limiting*. Certainly species can and do coexist while competing for some of the same resources. Nevertheless, Gause's theory predicts that when two species coexist on a long-term basis, either resources must not be limited or their niches will always differ in one or more features; otherwise, one species will outcompete the other and the extinction of the second species will inevitably result, a process referred to as **competitive exclusion**.

If resources are limiting, no two species can occupy the same niche indefinitely without competition driving one to extinction.

FIGURE 25.3
Competitive exclusion among three species of *Paramecium*. In the microscopic world, *Paramecium* is a ferocious predator. Paramecia eat by ingesting their prey; their cell membranes surround bacterial or yeast cells, forming a food vacuole containing the prey cell.

(a) In his experiments, Gause found that three species of *Paramecium* grew well alone in culture tubes. (b) But *Paramecium caudatum* would decline to extinction when grown with *P. aurelia* because they shared the same realized niche, and *P. aurelia* outcompeted *P. caudatum* for food resources. (c) However, *P. caudatum* and *P. bursaria* were able to coexist because the two have different realized niches and thus avoided competition.



Resource Partitioning

Gause's exclusion principle has a very important consequence: persistent competition between two species is rare in natural communities. Either one species drives the other to extinction, or natural selection reduces the competition between them. When the late Princeton ecologist Robert MacArthur studied five species of warblers, small insect-eating forest songbirds, he found that they all appeared to be competing for the same resources. However, when he studied them more carefully, he found that each species actually fed in a different part of spruce trees and so ate different subsets of insects. One species fed on insects near the tips of branches, a second within the dense foliage, a third on the lower branches, a fourth high on the trees and a fifth at the very apex of the trees. Thus, each species of warbler had evolved so as to utilize a different portion of the spruce tree resource. They *subdivided the niche*, partitioning the available resource so as to avoid direct competition with one another.

Resource partitioning is often seen in similar species that occupy the same geographical area. Such **sympatric species** often avoid competition by living in different portions of the habitat or by utilizing different food or other resources (figure 25.4). This pattern of resource partitioning is thought to result from the process of natural selection causing initially similar species to diverge in resource use in order to reduce competitive pressures.

Evidence for the role of evolution comes from comparison of species whose ranges are only partially overlapping. Where the two species co-occur, they tend to exhibit greater differences in **morphology** (the form and structure of an organism) and resource use than do their allopatric

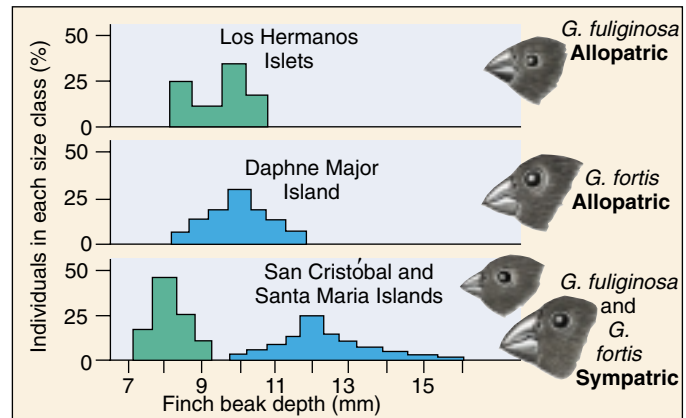


FIGURE 25.5
Character displacement in Darwin's finches. These two species of finches (genus *Geospiza*) have bills of similar size when allopatric, but different size when sympatric.

populations. Called **character displacement**, the differences evident between sympatric species are thought to have been favored by natural selection as a mechanism to facilitate habitat partitioning and thus reduce competition. Thus, the two Darwin's finches in figure 25.5 have bills of similar size where the finches are allopatric, each living on an island where the other does not occur. On islands where they are sympatric, the two species have evolved beaks of different sizes, one adapted to larger seeds, the other to smaller ones.

Sympatric species partition available resources, reducing competition between them.

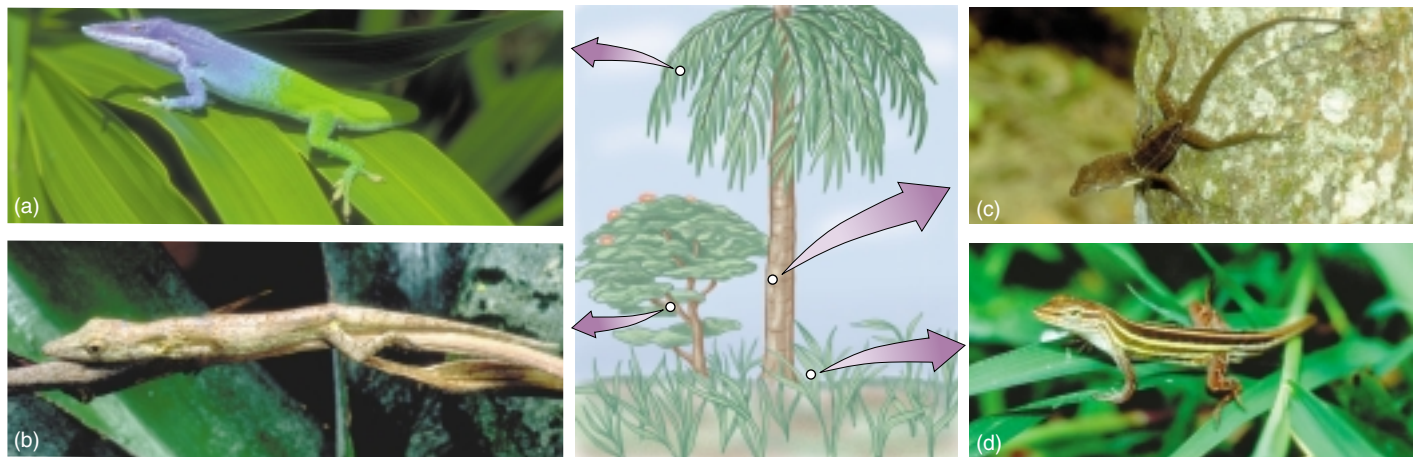


FIGURE 25.4
Resource partitioning among sympatric lizard species. Species of *Anolis* lizards on Caribbean islands partition their tree habitats in a variety of ways. Some species of anoles occupy the canopy of trees (a), others use twigs on the periphery (b), and still others are found at the base of the trunk (c). In addition, some use grassy areas in the open (d). When two species occupy the same part of the tree, they either utilize different-sized insects as food or partition the thermal microhabitat; for example, one might only be found in the shade, whereas the other would only bask in the sun. Most interestingly, the same pattern of resource partitioning has evolved independently on different Caribbean islands.